Catastrophic vegetation shifts and soil degradation in terrestrial grazing systems

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It has long been recognized that alternative vegetation states may occur in terrestrial grazing systems. This phenomenon may be of great importance as small environmental fluctuations may lead to relatively sudden and irreversible jumps between vegetation states. Early theoretical studies emphasized saturation of herbivore feeding to explain multiple stable states and catastrophic behaviour. Recent studies on semi-arid grasslands and arctic salt marshes, however, relate catastrophic events in these systems to plant–soil interactions.

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Many terrestrial grazing systems have proved to be vulnerable to changes in grazing pressure. Increase in human population size coincided with an increased grazing pressure by livestock in the Sahel region in Africa[1]. Livestock numbers, including cattle, sheep and goats, have increased from 40 million in 1950 to over 125 million in 1993. Resulting vegetation changes have been dramatic. The perennial grasses that were relatively abundant in the Sahel region were replaced by annual vegetation, which is very sensitive to disturbance[2]. In years with relatively low rainfall, this led to a collapse of the herbaceous vegetation[3,4], leaving a vegetation consisting of a sparse cover of unpalatable annual herbs and unpalatable shrubs[5]. Eventually, these processes resulted in desertification and famine in various parts of the Sahel region[5,6].

A collapse of the vegetation following changes in grazing pressure has also been reported for arctic plant communities along the coast of the Hudson Bay in Canada[7,8]. The mid-continent population of lesser snow goose (*Chen caerulescens caerulescens*) has increased from 1.2 million to almost two million birds between 1973 and 1989. This has resulted in a dramatic increase in the numbers of geese that breed on the salt marshes of the Hudson Bay coast. Increase in foraging and grubbing for roots and rhizomes in the soil has led to the destruction of existing plant communities and has created large bare patches lacking organic soil.

A number of ecological indicators point to the existence of multiple stable states in the systems described above[9]. First, increases in herbivore grazing pressure resulted in irreversible shifts between vegetation states in both the Sahel and along the Hudson Bay[1,8]. Attempts in the Sahel to restore the former vegetation in bare areas by reducing herbivore numbers had little effect; the areas have remained in their new barren state for at least 20 years and have not reverted to their original vegetated state[1,3,5]. Secondly, mosaics consisting of densely vegetated patches alternating with almost bare areas may also reflect multiple stable states[10]. These two-phase mosaics occur on different scales in semi-arid systems[11–13]. Two-phase mosaics are also found along the Hudson Bay, most likely resulting from intensive grazing and grubbing by lesser snow geese[14].

Similar phenomena have been described for other grazing systems around the world. Destruction of vegetation and subsequent desertification have been related to increased herbivore grazing pressure in other semi-arid regions in Africa[15,16], south-western USA[17], the Russian Federation[18], Australia[13,19] and in American salt marshes[20]. Additionally, a number of studies stress that overgrazed systems in Africa, America and Australia cannot easily be restored on a practical time-scale by simply lowering the level of herbivory[3,21,22].

The theoretical possibility of multiple stable states in terrestrial grazing systems has long been recognized[23,24]. Recent empirical studies have produced valuable insights into the causes of these phenomena. They may aid in the development of a general mechanistic framework for explaining catastrophic behaviour in terrestrial grazing systems.

Mechanistic explanations

Models that describe the dynamics of grazing systems are typically based on the same general structure[23,24]. The rate of change of plant standing crop P is represented by the differential equation:

$$\frac{dP}{dt} = G(P) - C(P)$$

in which $G(P)$ describes plant growth as a function of plant standing crop and $C(P)$ is the loss rate due to consumption by herbivores. For example, $G(P)$ may be given by the logistic growth equation, $G(P) = rP(1 - P/K)$, whereas losses due to overgrazing are proportional to both plant standing crop and herbivore density: $C(P) = \alpha HP$ (see Boxes 1 and 2). The models often incorporate H as a fixed parameter, that is, herbivore density is assumed to be more or less constant and independent of plant standing crop. This is not unreasonable for many managed grazing systems[25], but not necessarily applicable to more natural systems. In the example above, a single stable state is found independent of herbivore density (Fig. 1a). At low plant standing crop, plant growth exceeds grazer-induced losses. Beyond a certain plant standing crop (denoted by P_1), growth is lower than grazer-induced losses, because plant growth is limited by high vegetation density. Figure 1b shows that equilibrium plant standing crop P_e is negatively related to herbivore density. At high herbivore density, plants cannot compensate for herbivore induced losses, and consequently plants are unable to persist in the system.

This article reviews a number of mechanisms that produce multiple stable states in terrestrial grazing systems. Two groups of mechanisms are considered: mechanisms affecting the consumption term $C(P)$ and mechanisms affecting the growth term $G(P)$ (Ref. 25).

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Herbivore saturation

It is generally accepted that the rate of grazing is positively related to plant standing crop, eventually saturating at high plant standing crop[26–28]. Early studies on multiple stable states in grazing systems related discontinuous dynamical behaviour to herbivore saturation[23]. Herbivores are supposed to be relatively efficient in consuming plant biomass at low plant standing crop. As a consequence, plant losses exceed plant growth at low plant standing crop, which leads to further decline in plant standing crop when the system is sparsely vegetated (Fig. 1c). At intermediate plant standing crop, however, saturation of herbivore intake implies that plant growth exceeds herbivore-induced losses once plant standing crop exceeds a threshold level P_0. This results in a net increase in plant standing crop, until the upper equilibrium P_1 is reached. Beyond this upper equilibrium, net plant growth is negative due to limitations imposed by high vegetation density. Note that the steepness and convexity of the consumption curve are critical features influencing the existence of multiple stable states.

Figure 1d shows again how equilibrium plant standing crop is affected by herbivore density. At low herbivore density, only one stable equilibrium occurs. At intermediate herbivore densities, the model predicts that there are two stable states. One state is vegetated, whereas the other is barren due to overgrazing. At high herbivore densities, only the overgrazed state is possible. Hence, the vegetation inevitably collapses to the bare state when herbivore density is higher than the threshold level T_1. A sustainable vegetation state is not restored when herbivore density is diminished, unless density is reduced below a second threshold T_2.

Following Noy-Meir[23], a number of studies have stressed the importance of herbivore saturation for the existence of stable states and threshold effects. However, multiple stable states can also occur in the absence of herbivore saturation, that is, at a plant standing crop where herbivore saturation does not yet play a role. Various mechanisms, most notably soil degradation, depress plant growth at low plant standing crop (see Fig. 1e). As a result, the growth and consumption curves may intersect twice, even in the absence of herbivore saturation.

Box 1. Feedback between plant standing crop and water infiltration

Here, we present a simplified version of the water-limitation model analysed by Rietkerk and van de Koppel[33]. In semi-arid systems, plant growth is mainly limited by the availability of water[31]. Therefore, plant growth increases if water availability increases. Assume that the dynamics of the plant population P is characterized by the following differential equation:

$$\frac{dP}{dt} = rP(1 - \frac{P}{K})f(W) - \alpha HP$$

where r is a plant growth coefficient, K is the carrying capacity of the vegetation, $f(W)$ is a function describing the effect of water availability W on plant growth, α is a herbivore consumption coefficient and H is herbivore density. For example, $f(W)$ might be given by $f(W) = W/(W + b)$, where b determines how quickly growth increases with water availability.

The availability of soil water is governed by a number of factors, including water infiltration, losses of water from the soil due to evaporation and percolation, and the uptake of water by plants. The changes in water availability due to these factors may be represented by a differential equation:

$$\frac{dW}{dt} = W_0 \frac{P + aq}{P + a} \cdot eW - uWP$$

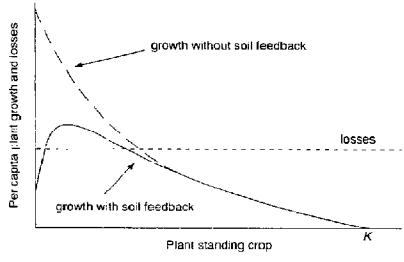
Here, water infiltration is an increasing but saturating function of plant standing crop P. W_0 stands for rainfall, a determines how quickly infiltration increases with plant standing crop, q is the fraction of rainfall that infiltrates into bare soils, e is the specific loss rate of water from the soil and u is a plant uptake coefficient. Since the dynamics of soil water act on a much faster time-scale than growth of plants, we assume soil water conditions to be in equilibrium with respect to plant growth (a quasi-steady-state approach[34]). The equilibrium condition $dW/dt = 0$ yields water availability $W^*(P)$ as a function of plant standing crop. In our example, $W^*(P)$ is given by

$$W^*(P) = W_0 \frac{P + aq}{P + a} \cdot \frac{1}{e + uP}$$

Insertion of $W^*(P)$ into the function f yields the plant growth curve:

$$G(P) = rP(1 - \frac{P}{K})f[W^*(P)]$$

which resembles the growth curve in Fig. 1c. Hence, multiple stable states and catastrophic changes between states are possible if water infiltration is positively related to plant standing crop. An alternative representation is given in the figure below which shows per capita growth $[G(P)/P]$ and losses $[C(P)/P]$ as a function of plant standing crop. The per capita rate of plant growth is reduced due to water limitation, relative to a model without soil feedback (obtained if $a = 0$).



Soil degradation

A large body of literature exists relating vegetation shifts in semi-arid grasslands to soil degradation[1,3,29–31]. Vegetation improves the structure and water-holding capacity of the soil, preventing crust formation through the interception of raindrops. Vegetation protects the soil against erosion by physical binding of soil, and the retention of surface water. Soil degradation occurs if plant standing crop is insufficient to prevent surface run-off of rain water. As a consequence, the proportion of the rainfall that infiltrates into the soil decreases[30]. Furthermore, run-off of water often leads to loss of nutrients via soil erosion[32]. Elwell and Stocking[29] showed that both run-off and soil erosion increase when vegetation cover decreases (see Fig. 2). In systems in which water or nutrients are limiting plant growth, as in most semi-arid regions, we may expect plant growth to decline when run-off and loss of nutrients occur.

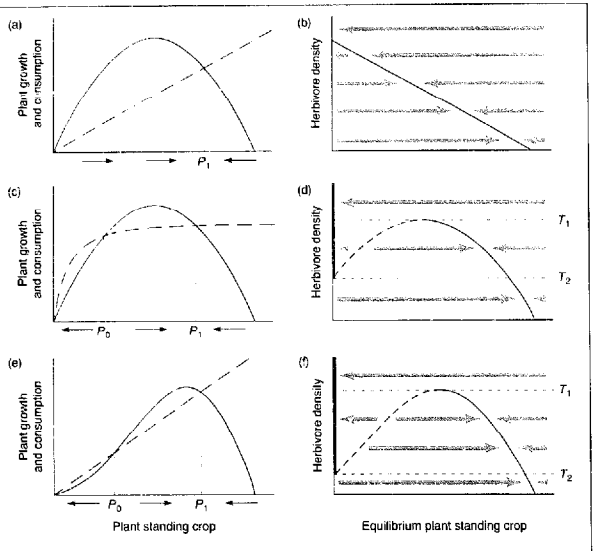


Fig. 1. (a), (c) and (e): Plant growth (solid line) and plant losses (dashed line) as a function of plant standing crop. In (a) and (c), plant growth is given by the logistic equation, whereas plant growth is depressed at low plant standing crop in (e). In all cases, the losses due to grazing are assumed to be proportional to herbivore density H. In (a) and (e), losses are proportional to plant standing crop, whereas they level off at high plant standing crop in (c) due to herbivore saturation. The intersects between both curves mark the equilibria. An increase of herbivore numbers results in a proportional increase in grazing pressure, and consequently plant loss curves become steeper, whereas they level off at higher values in (c), (b), (d) and (f): Relationship between equilibrium plant standing crop and herbivore density. (b) Only one equilibrium occurs. (d,f) For herbivore densities below T_1 or above T_2, there is a single stable equilibrium. For any herbivore density in between T_1 and T_2, two alternative stable equilibria occur. At the threshold values T_1 and T_2, discontinuous vegetation shifts may occur if herbivore numbers are increased or decreased respectively.

Walker *et al.*[5] modelled competition between woody vegetation and grasses for available soil water. Their model includes reduced water infiltration into the soil when the cover of grasses is low, as well as a saturating herbivore functional response. Two stable states emerge in their analysis: one state with both grasses and woody vegetation, and one degraded state with only woody vegetation. Treating the vegetation as a single state variable, Rietkerk and van de Koppel[33] show that herbivore saturation is not essential for this conclusion, since, in essence, reduced water infiltration at low plant standing crop is sufficient to explain catastrophic behaviour. These authors show that, in water limited systems, per capita plant growth may be reduced at low plant standing crop due to reduced water infiltration (see Box 1).

Similarly to the Sahel region, edaphic changes appear to be a key factor in the desertification of the salt marshes of the Hudson Bay. Srivastava and Jefferies[34] show that a positive feedback exists between plant standing crop and soil salinity, such that decreased plant standing crop increases soil salinity, which in turn decreases plant growth (Fig. 3). The decrease of plant standing crop by goose-grazing results in increased soil evaporation and deposition of salts in the upper layer of the soil[35,36]. The resulting saline soils inhibit the growth and survival of plants[14,34], thereby further reducing plant standing crop, in turn resulting in more bare soil. A simple model reveals that this feedback can reduce plant growth at low plant standing crop (see Box 2).

The implications of plant–soil feedbacks on the dynamics of grazing systems are illustrated by Figs 1e, f. At low plant standing crop, soil degradation occurs, resulting in reduced per capita plant growth, as is explained in Boxes 1 and 2. As a result, total plant growth $G(P)$ is upwardly convex at low plant standing crop. The growth and loss curves may now intersect twice (Fig. 1e). Plant growth is lower than plant losses at low plant standing crop, whereas it exceeds plant losses at intermediate plant standing crop. As a result, two stable states may occur within this system, even without saturating herbivore foraging. In one state, deteriorated edaphic conditions do not allow plants to compensate for losses, and this state lacks vegetation. Edaphic conditions are suitable for plant growth in the other state, allowing plants to compensate for grazer-induced losses; therefore, vegetation persists at this equilibrium.

This may trigger a positive feedback between reduced plant standing crop, reduced water and nutrient availability, and reduced plant growth.

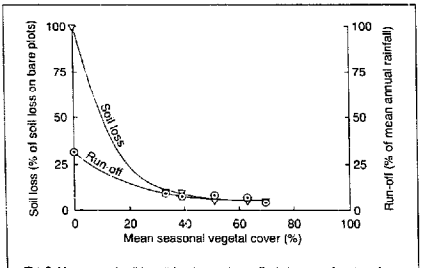


Fig. 2. Mean annual soil loss (triangles) and run-off (circles) as a function of vegetation cover. *Reproduced, with permission, from Ref. 29.*

The model yields predictions similar to the model with herbivore saturation. The system has a single vegetated state at low herbivore density. Two stable states occur at intermediate herbivore density. One state is bare, whereas the other is vegetated. At high herbivore density, plants cannot persist. Only one stable state exists, which is devoid of vegetation. There are, once again, two threshold herbivore densities T_1 and T_2 (Fig. 1f), at which catastrophic changes are to be expected if herbivore density is changed. Hence, soil degradation models offer an alternate mechanistic explanation for catastrophic vegetation shifts in terrestrial grazing systems.

A large number of soil-related processes may cause decreased per capita plant growth at low plant standing crop[10]. For instance, soil losses, due to wind erosion or run-off of water, may reduce nutrient availability at low plant standing crop[4,5]. Hence, per capita plant growth may be reduced when plant standing crop is low, especially in nutrient-limited systems[33]. The presence of dry or tough algal crusts may reduce shoot survival and leaf production, in particular on bare soils or in low density vegetation[16,17]. These algal crusts are rarely found in sites with abundant vegetation. Enhanced soil evaporation or high soil temperatures may also adversely affect plant growth on bare soils[14,35,38]. Changes in soil albedo may lead to reduced rainfall in bare regions as compared to vegetated regions[10]. These processes may cause positive feedbacks between plant growth and plant standing crop, and lead to vegetation collapse, even without increased herbivory. Herbivory may, however, expose these positive feedbacks by (1) reducing plant standing crop, which may result in soil degradation and hence in reduced plant growth, and (2) increasing plant losses, which make it more difficult for plants to cope with conditions that are deleterious for growth.

The systems described in this review have an important characteristic in common. In all cases, herbivore density increased independent of vegetation conditions. In the Sahel region, settlement of pastoral herdsmen in villages and around waterpoints caused increased grazing pressure on local vegetation, independent of within- and between-year changes in plant productivity[3]. Improved medical and veterinary aid (among other reasons) led to a rapid increase in livestock numbers. As a result, every settlement became the centre of its own desert[10]. On the arctic salt marshes, increased goose density resulted from decreased mortality on their wintering grounds and on the flyways. Despite the deterioration of vegetation, herbivore numbers remain high in both the Sahel and along the Hudson Bay. In grazing systems in which herbivore density is dependent on local plant standing crop, herbivore numbers may collapse once plant standing crop has diminished below a grazing threshold[41]. This, in turn, may prevent herbivores from severely disturbing their own food supply. Hence, these systems may be more resistant to increases in grazing pressure.

Conclusions

Two potential mechanisms for catastrophic vegetation shifts in terrestrial grazing systems are reviewed in this paper. The first is based on herbivore feeding characteristics, whereas the second is focused on plant–soil relationships. A number of empirical studies indicate that plant–soil feedbacks are the dominant cause of catastrophic behaviour in many terrestrial grazing systems. In these studies, a herbivore-induced decrease of plant standing crop has led to soil degradation and reduced plant growth. Positive feedback between reduced plant standing crop and deteriorated soil conditions has thereby contributed to irreversible veg-

Box 2. Feedback between plant standing crop and soil salt levels

A simple model for the interaction between soil salt levels and plant growth shows the potential for alternate stable states in the arctic salt marshes along the Hudson Bay. Srivastava and Jefferies[34] showed that per capita plant growth decreases with increasing salt levels (as is shown in Fig. 3b). Total net plant growth might therefore be given by a differential equation of the form:

$$\frac{dP}{dt} = rP\left(1 - \frac{P}{K}\right)f(S) - \alpha HP$$

where P is plant standing crop, r is the intrinsic growth rate of plants, K is the carrying capacity, $f(S)$ is a function describing the effect of the salt level S on plant growth, α is a herbivore consumption coefficient, and H is herbivore density. A simple example of a salt-limitation function is $f(S) = e^{-bS}$, where b is a scaling parameter.

Srivastava and Jefferies furthermore indicate that a negative relationship exists between salt levels in the soil and plant standing crop (Fig. 3a). This relation might be described by a function $S(P) = S_{max}\, e^{-cP}$, where S_{max} is the soil salt level when the soil is bare, and c is a scaling parameter. For the sake of simplicity, we assume that the salt level in the upper soil reacts rapidly upon plant standing crop. In this case, the salt level is a function $S(P)$ which upon insertion into the function f yields the plant growth curve:

$$G(P) = rP\left(1 - \frac{P}{K}\right)f[S(P)]$$

This growth function yields the growth curve in Fig. 1e. Hence, multiple stable states and catastrophic vegetation changes are possible if salt levels in the soil relate negatively to plant standing crop. Similarly to Box 1, the per capita rate of plant growth is reduced relative to a model without soil feedback, due to high salt levels at low plant standing crop.

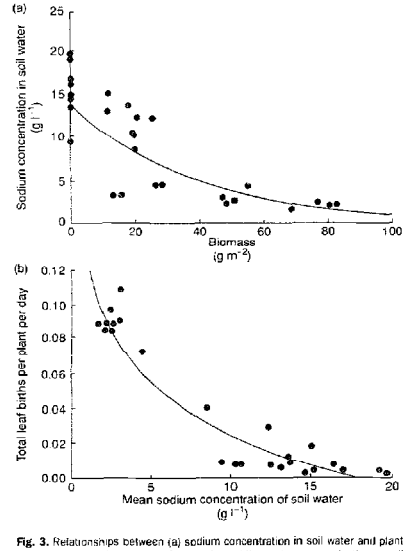


Fig. 3. Relationships between (a) sodium concentration in soil water and plant standing crop, and (b) total leaf birth rate and the sodium concentration in soil water, in an arctic coastal salt marsh. *Reproduced, with permission, from Ref. 34.*

etation destruction. It is conceivable that both mechanisms act simultaneously in many natural systems.

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References

1 Le Houérou, H.N. (1989) *The Grazing Land Ecosystem of the African Sahel*, Ecological Studies, Vol. 75, Springer-Verlag

2 Breman, H. *et al.* (1980) **Pasture dynamics and forage availability in the Sahel**, *Isr. J. Bot.* 28, 227–251

3 Sinclair, A.R.E. and Fryxell, J.M. (1985) **The Sahel of Africa: ecology of a disaster**, *Can. J. Zool.* 63, 987–994

4 Schlesinger, W.H. *et al.* (1990) **Biological feedbacks in global desertification**, *Science* 247, 1043–1048

5 Walker, B.H. *et al.* (1981) **Stability of semi-arid savanna grazing systems**, *J. Ecol.* 69, 473–498

6 Graetz, R.D. (1991) **Desertification: a tale of two feedbacks**, in *Ecosystem Experiments* (Mooney, H.A. *et al.*, eds), pp. 59–87, John Wiley & Sons

7 Jefferies, R.L. (1988) **Vegetational mosaics, plant–animal interactions and resources for plant growth**, in *Plant Evolutionary Biology* (Gottlieb, L.D. and Jain, S.K., eds), pp. 341–369, Chapman & Hall

8 Jefferies, R.L. (1988) **Pattern and process in arctic coastal vegetation in response to foraging by lesser snow geese**, in *Plant Form and Vegetation Structure* (Werger, M.J.A., ed.), pp. 281–300, SPB Academic Publishing

9 Rietkerk, M. *et al.* (1996) **Sahelian rangeland development: a catastrophe?** *J. Range Manage.* 49, 512–519

10 Wilson, J.B. and Agnew, A.D.Q. (1992) **Positive-feedback switches in plant communities**, *Adv. Ecol. Res.* 23, 263–336

11 Belsky, A.J. (1986) **Population and community processes in a mosaic grassland in the Serengeti, Tanzania**, *J. Ecol.* 74, 841–856

12 Montana, C. (1992) **The colonization of bare areas in two-phase mosaics of an arid ecosystem**, *J. Ecol.* 80, 315–327

13 Ludwig, J.A. and Tongway, D.J. (1995) **Spatial organisation of landscapes and its function in semi-arid woodlands, Australia**, *Landscape Ecol.* 10, 51–63

14 Srivastava, D.S. and Jefferies, R.L. (1995) **Mosaics of vegetation and soil salinity: a consequence of goose foraging in an arctic salt marsh**, *Can. J. Bot.* 73, 75–83

15 Milton, S.J. and Dean, W.R.J. (1995) **South Africa's arid and semiarid rangelands: why are they changing and can they be restored?** *Environ. Monit. Assess.* 37, 245–264

16 Kerley, G.I.H., Knight, M.H. and De Kock, M. (1995) **Desertification of subtropical thicket in the Eastern Cape, South Africa: are there alternatives?** *Environ. Monit. Assess.* 37, 211–230

17 Hess, K. and Holechek, J.L. (1995) **Policy roots of land degradation in the arid region of the United States: an overview**, *Environ. Monit. Assess.* 37, 123–141

18 Zonn, I.S. (1995) **Desertification in Russia: problems and solutions (an example in the republic of Kalmykia-Khalmg Tangch.** *Environ. Monit. Assess.* 37, 347–363

19 Ludwig, J.A. and Tongway, D.J. (1995) **Desertification in Australia: an eye to grass roots and landscapes**, *Environ. Monit. Assess.* 37, 231–237

20 Miller, D.L., Smeins, F.E. and Webb, J.W. (1996) **Mid-Texas coastal marsh change (1939–1991) as influenced by lesser snow goose herbivory**, *J. Coastal Res.* 12, 462–476

21 Friedel, M.H. (1991) **Range condition assessment and the concept of thresholds: a viewpoint**, *J. Range Manage.* 44, 422–426

22 Laycock, W.A. (1991) **Stable states and thresholds of range condition on North American rangelands: a viewpoint**, *J. Range Manage.* 44, 427–433

23 Noy-Meir, I. (1975) **Stability of grazing systems: an application of predator–prey graphs**, *J. Ecol.* 63, 459–481

24 Yodzis, P. (1989) *Introduction to Theoretical Ecology*, Harper & Row

25 Clark, C.W. (1990) *Mathematical Bioeconomics: The Optimal Management of Renewable Resources* (3rd edn), John Wiley & Sons

26 Holling, C.S. (1959) **The components of precation as revealed by a study of small-mammal predation of the European pine sawfly**, *Can. Entomol.* 91, 293–320

27 Short, J. (1985) **The functional response of kangaroos, sheep and rabbits in an arid grazing system**, *J. Appl. Ecol.* 22, 435–447

28 Spalinger, D.E. and Hobbs, N.T. (1992) **Mechanisms of foraging in mammalian herbivores: new models of functional response**, *Am. Nat.* 140, 325–348

29 Elwell, H.A. and Stocking, M.A. (1976) **Vegetal cover to estimate soil erosion hazard in Rhodesia**, *Geoderma* 15, 61–70

30 Kelly, R.D. and Walker, B.H. (1976) **The effects of different forms of land use on the ecology of a semi-arid region in south-eastern Rhodesia**, *J. Ecol.* 64, 553–576

31 Breman, H. and De Wit, C.T. (1983) **Rangeland productivity and exploitation in the Sahel**, *Science* 221, 1341–1347

32 Kiepe, P. (1995) *No Runoff, no Soil Loss: Soil and Water Conservation in Hedgerow Barrier Systems*, Tropical Resource Management Papers no. 10, Wageningen Agricultural University, The Netherlands

33 Rietkerk, M. and van de Koppel, J. (1997) **Alternate stable states and threshold effects in semi-arid grazing systems**, *Oikos* 79, 69–76

34 Srivastava, D.S. and Jefferies, R.L. (1996) **A positive feedback: herbivory, plant growth, salinity, and the desertification of Arctic salt-marsh**, *J. Ecol.* 84, 31–42

35 Iacobelli, A. and Jefferies, R.L. (1991) **Inverse salinity gradients in coastal marshes and the death of stands of *Salix*: the effects of grubbing by geese**, *J. Ecol.* 79, 61–73

36 Srivastava, D.S. and Jefferies, R.L. (1995) **The effects of salinity on the leaf and shoot demography of two arctic forage species**, *J. Ecol.* 83, 421–430

37 Grootjans, A.P., van den Ende, F.P. and Walsweer, A.F. (1997) **The role of microbial mats during primary succession in calcareous dune slacks: an experimental approach**, *J. Coastal Conserv.* 3, 95–102

38 Belnap, J. (1995) **Surface disturbances: their role in accelerating desertification**, *Environ. Monit. Assess.* 37, 39–57

39 Charney, J., Stone, P.H. and Quirk, W.J. (1975) **Drought in the Sahara: a biogeographical feedback mechanism**, *Science* 187, 434–435

40 Wade, N. (1974) **Sahelian drought: no victory for western aid**, *Science* 185, 234–237

41 Drent, R.H. and Prins, H.H.T. (1987) **The herbivore as prisoner of its food supply**, in *Disturbance in Grasslands* (Van Andel, J. *et al.*, eds), pp. 131–147, Dr. W. Junk Publishers

42 Edelstein-Keshet, L. (1988) *Mathematical Models in Biology*, McGraw-Hill